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Assembly of plant communities in coastal wetlands—the role of saltcedar *Tamarix chinensis* during early succession

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Abstract

Aims
The mechanisms of plant community assembly are hypothesized to vary at different stages of succession. Here, we explore the local assemblage structure of a herbaceous plant community at its early stage of succession in a supratidal wetland. Specifically, we assess the role of Chinese saltcedar (*Tamarix chinensis*), the lone dominant shrub species, in shaping the spatial structure and species composition in the local plant community, after landscape alteration.

Methods
We used the multivariate trend-surface analysis for analyzing the spatial structure of the community composition. A null model was also used to detect potential biotic interactions between species. Statistical significance was derived from a permutation test by randomizing the presence-absence matrix and functional traits independently. Sensitivity analysis by randomly selecting 50 subplots and repeating the null model tests was also done. Finally, rank correlation analysis was used to study the relationship between effect sizes and distance to nearest *T. chinensis* individuals.

Important Findings
The herbaceous plant community was highly structured and shaped by the presence of *T. chinensis*. At local scale, two functional traits, plant height and leaf area, were found to be significantly convergent. Dispersal, environmental stress and interspecific competition played a trivial effect on the local community assembly. The facilitating effect of *T. chinensis* on the pioneering herbaceous plants, through acting as a wind shelter, was put forward as the dominant community assembly process.

Keywords supratidal wetland, functional traits, spatial structure, trait convergence, facilitative effect, wind sheltering

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INTRODUCTION

Species assemblages in plant communities are not random, and such non-random patterns of species composition can be caused by multiple ecological processes working at different scales (Dray *et al.* 2012). The term 'assembly rule' was first introduced to ecology by Diamond (1975) to account for the non-random species composition, and later extended to include any constraints on species coexistence (Götzenberger *et al.* 2012). To date, the quest for general assembly rules in plant communities remains a major challenge in community ecology (Ackerly 2003; Bruun and Moen 2003; Fargione *et al.* 2003; Hillebrand and Matthiessen 2009; Hubbell 2001; Hui *et al.* 2013; Sargent and Ackerly 2008).

In principle, the assembly rules can be classified into phylogeographic and ecological rules, which represent the most recent model of community assembly processes (HilleRisLambers *et al.* 2012). Phylogeographic assembly rules refer to historical processes, including evolution, that contribute to the formation of regional species pools (Götzenberger *et al.* 2012; HilleRisLambers *et al.* 2012). Ecological assembly rules include dispersal, biotic interactions and abiotic environmental factors, and these assembly rules are related to spatial scales (Götzenberger *et al.* 2012). Species from a regional species pool are filtered by their dispersal capabilities to constitute the local species assemblage, whereas species in a local community need to pass through multiple abiotic environmental and biotic filters to become established (Belyea and Lancaster 1999; Chase 2003; Götzenberger *et al.* 2012; Hui *et al.* 2011). Moreover, community assembly rules also vary in different stages of succession (Cottenie 2005; Götzenberger *et al.* 2012; Leibold *et al.* 2004). For instance, in the initial phase of succession, dispersal could be the predominant assembly process, whereas biotic filtering elicits stronger responses as succession advances (Navas and Violle 2009; Weiher and Keddy 1999). Evidence from phylogenetic analysis also suggested that environmental filtering or disturbance might determine community assembly during succession (Norden *et al.* 2012; Whitfeld *et al.* 2012; Zhang *et al.* 2014).

To assess ecological assembly rules, species non-random assemblages in local communities are often examined in two aspects: spatial and ecological dispersion (Götzenberger *et al.* 2012). Spatial dispersion of a plant community indicates the spatial association or dissociation of resident species (Hui 2009) and is quantified *via* spatial structure analysis. Ecological dispersion indicates the ecological similarity or dissimilarity of, say, the functional traits between species, where 'divergence' and 'convergence' are the two opposite directions of functional trait dispersion (Kraft *et al.* 2008; Stubbs and Wilson 2004). Trait convergence reflects shared ecological tolerances of species in the assemblage and has been interpreted to be a result of environmental filtering (Ackerly and Cornwell 2007; Cornwell *et al.* 2006). Trait divergence indicates the evidence of limiting similarity (Watkins and Wilson 2003) and often suggests that the resident species in the assemblage are arranged by their resource-acquisition/consumption traits so that competing species can easily coexist through niche differentiation (Macarthur and Levins 1967; Stubbs and Wilson 2004).

Null model tests that compare certain parameters of an observed community data set with the same parameters in multiple randomized community data sets were widely used for detecting the non-random component in species composition (Cornnor and Simberloff 1979; Gotelli 2000; Hui and McGeoch 2014). The term 'null models' refers to the fact that the model was considered to represent the null hypothesis, where the observed pattern is a product of chance alone. Götzenberger *et al.* (2012) summarized four classes of null model approaches for assessing ecological assembly rules: co-occurrence approach, niche limitation approach, guild proportionality approach and limiting similarity approach. The co-occurrence approach tests whether local communities are subject to interspecific competition based on the theoretical assumption that competitive exclusion reduces the number of possible species co-occurrences (Gotelli and Graves 1996; Stone and Roberts 1990). Environmental heterogeneity is considered to be a constraint of co-occurrence approaches (Götzenberger *et al.* 2012). Niche theory predicted that the number of species in a community was limited by the number of niches, and the evidence for niche limitation can be tested by comparing the observed and expected variation in species richness or diversity (Wilson *et al.* 1987; Zobel and Zobel 1988). The above-mentioned two approaches were referred to as species-based approach because only presence-absence or abundance community data sets were used (Götzenberger *et al.* 2012). Because competition is expected to be greatest within functional guilds, the number of species within different functional guilds, or the total abundance of a particular guild in a community, is assumed to be constant among patches (Bossuyt *et al.* 2005; Wilson *et al.* 2000). If both abundance data and trait data are available, it is possible to assess the degree of constancy in the number and proportion of species within functional guilds. Furthermore, by examining the dissimilarity between species in a community in terms of functional traits, we can test whether species traits in the community are more similar or dissimilar than would be expected by chance (Kraft *et al.* 2008; Stubbs and Wilson 2004). The latter two null model approaches are referred to as trait-based approaches in literature (Götzenberger *et al.* 2012). For a specific biological question, selecting an appropriate null model and interpreting the outcome correctly are the key to successful application of null model approaches (Gotelli and Graves 1996; Götzenberger *et al.* 2012).

We here focus on examining the ecological assembly rules of a herbaceous plant community in Eastern China, i.e. still in its early stage of succession. The plant community is located in a supratidal wetland, which used to be an intertidal zone. The vegetation has started changing after a seawall was built to block seawater from entering this wetland. As the soil salinity was extremely high before introduction of the embankment, only two salt-tolerant plant species could survive: *Suaeda salsa* and *Tamarix chinensis* (Chinese tamarisk). After building the embankment, soil salinity gradually declined, from rainwater leaching, to 0.1% enabling 12 grass species to be successfully established, such as *Artemisia capillaris, Setaria viridis* and *Phragmites australis*, which then competitively excluded *S. salsa* from the wetland (Bi *et al.* 2014). As these colonizing species can produce a large quantity of seeds that are capable of travelling long distances by wind, limited dispersal is unlikely an important assembly rule, especially at relatively small spatial scales (Götzenberger *et al.* 2012; Schleicher *et al.* 2011). As such, abiotic environmental filters and biotic interactions could be important assembly processes in this plant community. Consequently, we aim to explore the spatial structure

and assembly rules of this herbaceous plant community at a relatively small spatial scale. Null model approaches will be used for community assembly. As *T. chinensis* is the only shrub and a dominant species in both the regional intertidal and supratidal wetlands, we further assess its role in shaping the spatial structure and species composition in the local plant community, after the landscape alteration by human activities. To this end, this study is relevant to both testing local assembly rules and facilitating regional wetland management.

MATERIALS AND METHODS

Study area

The study area is located in the southern coast of Laizhou Bay within the Changyi National Marine Protection Area (37°07′N, 119°36′E) in Shandong province, Eastern China (Fig. 1). The area has a continental monsoon climate, with average temperatures ranging from −3.8°C in January to 25.9°C in July. Annual average precipitation is 628 mm, whereas annual average evaporation is 1776 mm. The annual sunshine duration is 2428 h. Strong winds usually occur in spring, sometimes reaching speeds of 20 m/s. The yearly average wind speed is 3 m/s, but the maximum average wind speed can reach 18 m/s. This coastal area is a wide plain declining from south to north, with gentle slope of 0.2‰. The sampling area is about 1 m below the sea level (Fig. 1).

Data collection

The mean density of *T. chinensis* in the whole protection area is 0.16/m^2, with a mean height of 1.64 (±0.67) m and a crown diameter of 1.56 (±0.49) m. The field survey was conducted in mid-September 2013, the end of the growing season for wetland plant species. The sampling site was located 600 m, toward the inland direction, from the seawall that was built in 2010. To avoid any human disturbance, the sampling site was selected to be >30 m away from any brine wells, roads and water canals. In this paper, we are specifically interested in biotic assembly rules during early succession, which are expected to work at relatively small scales (Bycroft *et al.* 1993). Therefore, a 10 × 10-m plot, which covers three mature *T. chinensis* bushes, was surveyed (Fig. 2), with their crown diameters being 3.6, 1.8 and 1.2 m, respectively. The plot size is large enough to represent a local herbaceous plant community, with all common plant species in the wetland present, but small enough to discard the effect of habitat heterogeneity. The plot was further divided into one hundred 1 × 1-m subplots, and the abundance of each vascular plant species was counted within each one. We did not measure the soil characteristics for all subplots as the soil profile is nearly homogeneous within the 10 × 10-m plot (Bi *et al.* 2014). Two functional traits, plant height and leaf area, were measured for 10 individuals of each plant species within the subplot. Plant height is an important functional trait associated with light competition (Anten and Hirose 1999; Gallapher *et al.* 2011), and leaf area is related to heat load, water retention and gas exchange (Schulze *et al.* 1996).

Spatial structure analysis

A modeling-oriented approach, specifically the multivariate trend-surface analysis, was used for the spatial structure analysis. Multivariate trend-surface analysis is an adaption of trend surface to canonical ordination and allows one to extract the spatial

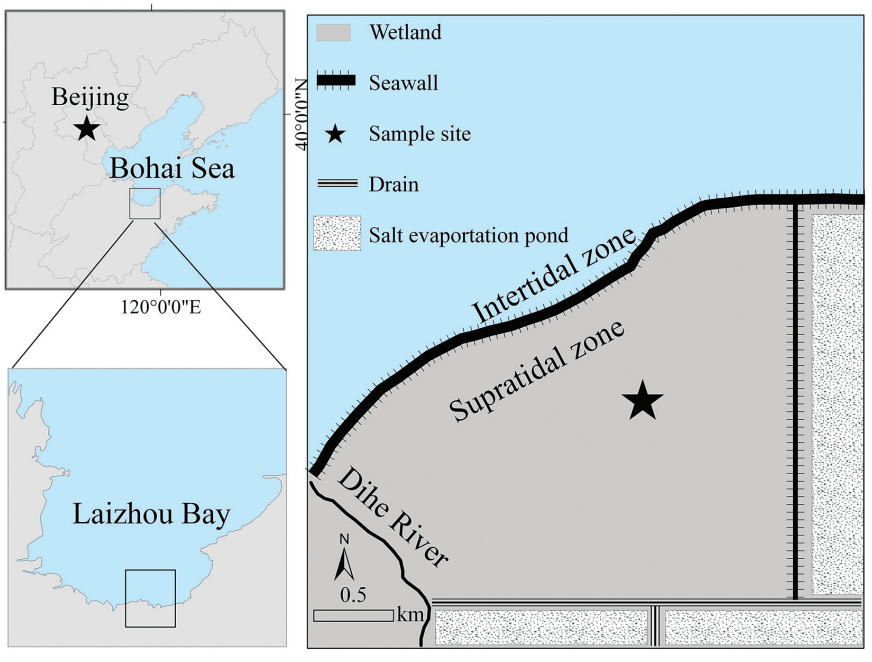

Figure 1 : location of the study area. The supratidal wetland used to be an intertidal zone and submerged by tide water. The outer seawall was constructed in 2010 when the plant community succession started.

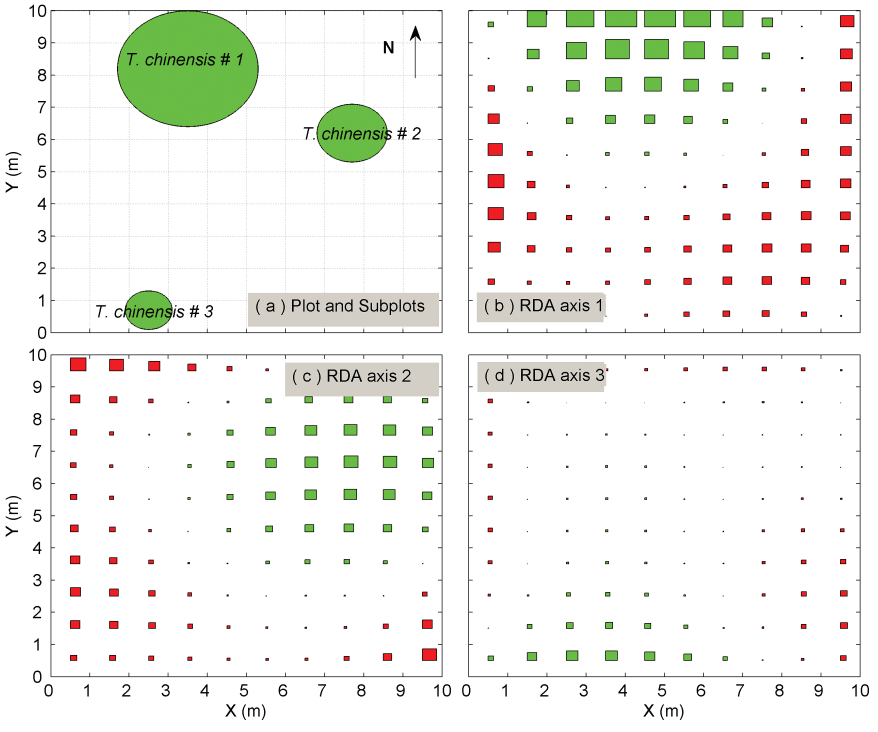

Figure 2 : the sampling site and results of the spatial analysis of the herbaceous plant community. (**a**) The 10- × 10-m plot and three mature *T. chinensis* individuals. (**b–d**) Three significant canonical axes of RDA represent linearly independent spatial structures. Green and red squares correspond to positive- and negative-fitted site scores, respectively. The size of squares represents the absolute value of fitted site score.

structure of ecological data (Borcard *et al.* 2011). The key idea of multivariate trend-surface analysis is to explain the composition variation in the plant community using polynomial functions of the subplot coordinates (Borcard *et al.* 1992). We restricted the polynomials to the third degree and applied the canonical ordination by means of redundancy analysis (RDA). The forward selection method was used to reduce the model to include only significant components (Blanchet *et al.* 2008), with double stopping criterion applied and no monomials eliminated. Data of species abundance were transformed using the Hellinger transformation before analysis (Legendre and Gallagher 2001), and the statistical significance was tested using a permutation test.

Null model and sensitivity analysis

Co-occurrence analysis was firstly used here to evaluate whether local herbaceous plant communities were subject to interspecific competition (Adams 2007; Gotelli and McCabe 2002; Jenkins 2006; Zhang *et al.* 2009). In this paper, we chose C-score as the index of species co-occurrence patterns (Stone and Roberts 1990). If an assemblage is structured by competition, observed communities should contain a larger C-score than expected by chance (Gotelli and Ellison 2002). The fixed-equiprobable algorithm was used to randomize the presence-absence matrix of the local herbaceous plant community, where row sums were fixed in order that each species occurred with the same frequency in the randomly constructed assemblages as in the observed assemblage, whereas all columns were equiprobable. Gotelli (2000) recommended this algorithm when analyzing samples collected in areas of homogenous habitat. In this study, the presence-absence matrix was randomized 3000 times and the observed C-score was considered significant when it was greater or less than 95% of the randomly generated C-scores.

The null model approach was further used for investigating the divergence or convergence of the functional traits (Schamp *et al.* 2008; Stubbs and Wilson 2004). Specifically, we randomized trait data but conserved species richness and abundance within subplot. This null model thus tests whether observed trait distributions differ significantly from those expected from randomly assigning traits to species (Schamp *et al.* 2008). We chose four metrics to analyze the dispersion of functional traits: mean, range, mean nearest trait distance (meanNTD) and variance in nearest trait distance (varNTD, Schamp and Aarssen 2009; Schamp *et al.* 2011; Stubbs and Wilson 2004). The first test statistic, *mean*, was used to assess whether one end of a given trait is favored or not (Schamp and Aarssen 2009; Schamp *et al.* 2011). A significantly larger range or higher meanNTD than null expectation indicates trait divergence and supports the limiting similarity theory (Weiher and Keddy 1995), whereas a significantly smaller range or lower meanNTD indicates trait convergence (Grime 2006; Schamp and Aarssen 2009). A low value of varNTD can also be indicative of limiting similarity (Schamp and Aarssen 2009; Stubbs and Wilson 2004). Functional traits were firstly log-transformed and standardized in null model tests (Stubbs and Wilson 2004). In each case, the statistic was calculated for

each plot and trait, and the average of plot-level statistic was used as the test statistic (Schamp and Aarssen 2009; Schamp *et al.* 2011). Abundance data were not used in the computation of test statistics. The distributions of these four test statistics were generated from 3000 independent randomizations of the null model. A two-tail test was selected, with the *P*-values calculated as *P* = MIN [2S/3001; 2L/3001], where S and L refer to the number of runs among the 3000 runs of the null model with its metrics smaller or larger, respectively, than the observed metrics (Bersier and Sugihara 1997).

Due to the relatively small size of the study area, spatial autocorrelation could play an important role in calculating compositional similarity and thus potentially affects the reliability of the above null model analyses. To test whether spatial autocorrelation had an impact on the results of the null model analyses, a sensitivity analysis was done by having 1000 runs of the null model but for only 50 subplots randomly selected from all 100 subplots. Only when the results from the sensitivity analysis were consistent with the 3000 runs of the null model for all 100 subplots, the statistical tests of the latter null model test were considered to be reliable.

Rank correlation analysis

To further illustrate how the presence of *T. chinensis* affected the spatial distribution and functional trait dispersion of herbaceous plant species, the simple linear regression and rank correlation methods were applied. Firstly, we calculated the mean of functional traits (plant height and leaf area) for each herbaceous plant species in each subplot, and then calculated the distances from the center of this subplot to the three *T. chinensis* individuals, respectively. A linear regression analysis was run between the mean of functional traits and the distance from the subplot center to the nearest *T. chinensis* individual. In total, we selected seven abundant herbaceous plant species. Next, rank correlation analysis was used here to test whether the dominant shrub species, *T. chinensis*, affects the assembly of herbaceous plant communities in terms of plant height and leaf area. The approach was originally introduced for testing how functional traits change along environmental gradients (Schamp and Aarssen 2009). For simplicity, the distance from the subplot center to the nearest *T. chinensis* individual was transformed into an ordinal variable, ranging from the shortest distance (Class 1) to the farthest distance (Class 4). In this study, rank correlations were used to compare effect sizes (z-scores) of different distance classes. For each subplot and test statistic, z-scores were calculated as (O-M)/S (Schamp and Aarssen 2009), where O represents the observed value of the test statistic, M and S represent the mean and standard deviation of the test statistic from 3000 randomized communities.

RESULTS

The multivariate trend-surface analysis showed that the herbaceous plant community was highly structured, with three significant spatial components identified (Fig. 2). The first RDA axis (71.5% variance explained) represents the influence of the largest *T. chinensis* individual on the spatial structure of the community (Fig. 2b). The second and third RDA axes (16.2% and 8.1% variance explained, respectively) represent the impacts of the other two *T. chinensis* individuals on the community structure (Fig. 2c and d). These three canonical axes account for 96% of the explained variance and provide obvious evidence that the species assemblage in this herbaceous plant community was not randomly distributed in space but shaped by the presence of *T. chinensis*.

In the co-occurrence analysis, we found that the observed C-score was not significantly greater than that expected by chance (*P* = 0.673) providing no evidence for competitive-based community assembly. To test whether autocorrelation may have impacted the above result, the null model was run 1000 times with only 50 randomly selected subplots. For these 1000 null model tests, the results were as follows: 46 significant C-scores ($P < 0.05$) and 954 non-significant C-scores ($P > 0.05$), suggesting that the spatial autocorrelation did not affect the statistical results and conclusions from the co-occurrence analysis. That is, the observed C-score was not significantly greater than that expected by chance.

Null model analysis for the functional trait, 'plant height', showed that herbaceous plant species within subplots were significantly taller than expected by chance, supporting a size-advantage in competition ($P < 0.001$, Table 1). The value of test statistics, range and mean NTD, for plant height of the observed herbaceous plant community was significantly lower than the expected value (*P* = 0.001 and 0.002, Table 1), suggesting that locally coexisting species have rather similar plant height, thus supporting trait convergence. Meanwhile, the plant height of herbaceous plant species was no more evenly spaced than expected (*P* = 0.278, Table 1). Sensitivity analysis further showed that the results of most statistical tests with 50 randomly selected subplots were consistent with that of statistical test using all 100 subplots (Table 2).

Null model analysis of leaf area showed a similar result except for the first test statistic. The mean of leaf area was neither larger nor smaller than expected by chance (*P* = 0.601, Table 1). Specifically, the range of plant leaf area was significantly smaller than expected, supporting trait convergence (*P* = 0.002, Table 1). Moreover, the leaf areas of coexisting plant species were more similar to each other (i.e. meanNTD was lower than expected by chance, *P* = 0.002, Table 1), which conformed to the prediction from trait convergence. The observed value of varNTD did not differ from the null expectation (*P* = 0.547, Table 1). Again, sensitivity analysis verified that the above results were not driven by spatial autocorrelation (Table 2).

Linear regression analysis showed that the species-specific relationship between species abundance and their distance to the nearest *T. chinensis* showed one significantly negative and two significantly positive relationships, with the other four relationships statistically non-significant (Table 3). For the relationship between plant height and distance, there were six significantly negative relationships, and one non-significant

Table 1 : ecological dispersion of functional traits

Trait	Index	*P*-value	Obs vs. Exp	Theory supported
Plant height	Mean	**<0.001**	**Obs > Exp**	**Size-advantage**
	Range	**0.001**	**Obs < Exp**	**Trait convergence**
	meanNTD	**0.002**	**Obs < Exp**	**Trait convergence**
	varNTD	0.278	Obs < Exp	
Leaf area	Mean	0.601	Obs < Exp	
	Range	**0.002**	**Obs < Exp**	**Trait convergence**
	meanNTD	**0.002**	**Obs < Exp**	**Trait convergence**
	varNTD	0.547	Obs < Exp	

Abbreviations: exp = expected, obs = observed.
Tests of the difference between obs and exp traits are based on 3000 independent randomizations, with bold values indicating the significance at $\alpha = 0.05$.

Table 2 : sensitivity analysis based on 1000 statistical tests using the null model

		Obs < Exp		Obs > Exp	
Trait	Index	Significant	No significant	Significant	No significant
Plant height	Mean	0	46	**921**	33
	Range	**875**	116	4	5
	meanNTD	**832**	131	2	35
	varNTD	26	**691**	37	246
Leaf area	Mean	143	446	122	389
	Range	**793**	115	3	89
	meanNTD	**801**	127	13	59
	varNTD	29	**526**	18	427

Abbreviations: exp = expected, obs = observed.
The tests are similar to that described in Table 1 except that in each test only 50 subplots are randomly chosen from all 100 subplots. The number in the table is the number of statistical tests at a significance level of 0.05.

relationship (Table 3). Finally, there were two significantly negative and four non-significant relationships between the mean leaf area of herbaceous plant species and the distance to the nearest *T. chinensis* individual (Table 3).

Rank correlation analysis showed that the effect sizes of the test statistic, mean, changed significantly among subplots that belong to different distance classes (Fig. 3 and Table 4). Both plant height and leaf area decreased with the increasing distance to the nearest *T. chinensis* individual (rho = −1.2782, $P < 0.0001$ and rho = −0.7501, $P = 0.0008$, respectively). Effect sizes of other test statistics did not change significantly with the distance to the nearest *T. chinensis* individual (Table 4).

DISCUSSION

Assembly of herbaceous plant community at local scale in wetland

Here, we explored the local assemblage structure of a herbaceous plant community at its early stage of succession in a supratidal wetland. During this early succession, plant species *S. salsa* that lives in salt marsh habitats was competitively excluded by terrestrial plants (*A. capillaris*, *S. viridis* and *P. australis*) from the regional species pool. These cloning terrestrial species have a similar strategy of wind dispersal seeds, consistent with the prediction that wind dispersal is the main and favored dispersal vector in the early succession stage (Donaldson *et al.* 2014; Prach and Pyšek 1999; Schleicher *et al.* 2011; Wilson *et al.* 2014). This study only surveyed a 10- × 10-m plot with 8 species discovered out of the 12 regional colonizing plant species. At this small spatial scale, the effect of dispersal on community assembly is trivial as all these species are strong dispersers.

We have analyzed the assembly of the herbaceous plant community with respect to two functional traits, plant height and leaf area, which are related to the capability of light capture, heat load, water retention and gas exchange (Anten and Hirose 1999; Givnish and Vermeij 1976; Schulze *et al.* 1996; Stubbs and Wilson 2004). In some previous studies, coexisting wetland species were found to be more diverse in height than expected (Weiher *et al.* 1998) and that herbaceous plant species are organized randomly with respect to maximum height among plots within an old-field forest (Schamp *et al.* 2008). However, we found that the herbaceous plant community was organized non-randomly with respect to plant height and leaf area. Specifically, we found strong evidence for convergence of plant height and leaf area, which is consistent with the finding in most studies using null model approaches in plant community ecology, opposing rather than supporting limiting similarity theory (Schleicher *et al.* 2011). The potential impact of autocorrelation on compositional similarity and functional traits dispersion was excluded based on sensitivity analyses.

At local scales, environmental stress and strong competition could be two possible filters that induce functional trait convergence (Grime 2006; Weiher and Keddy 1995). As soil in the wetland is a mixture of sand, clay and fragmented seashells, its capacity for water retention is very low. The soil is also salty and dry from excessive saline groundwater exploitation by humans (Bi *et al.* 2014). Although we did not measure the functional traits related to stress tolerance, the colonizing plant species in the wetland are expected to be filtered by the salty and dry soil environment. In the 10- × 10-m plot of this study, the soil environment is homogeneous, with no obvious gradients of soil nutrients and water content (Bi *et al.* 2014). Consequently, we did not explain the spatial variation of community assemblage by soil characteristics. Although strong interspecific competition can induce functional trait convergence, this biotic interaction filter only occurs at late succession stages, when competitive exclusion has done its work (Grime 2006; Schleicher *et al.* 2011; Tilman 1990). Therefore, interspecific competition can be ruled out from the assembly rules at this early succession stage of the herbaceous plant community. Co-occurrence analysis also verified this point.

Table 3 : the relationships between distance to the nearest *T. chinensis* individual and the abundance (and functional traits) of seven herbaceous plant species

Species	Abundance vs. distance			Plant height vs. distance			Leaf area vs. distance		
	Relationship	r^2	*P*-value	Relationship	r^2	*P*-value	Relationship	r^2	*P*-value
Conyza canadensis	Positive	0.088	**0.004**	Negative	0.196	**<0.001**	Negative	0.072	**0.01**
Taraxacum brassicaefolum Kitag.	N.S.	0.003	0.702	Negative	0.230	**<0.001**	N.S.	0.007	0.634
Setaria viridis	N.S.	0.051	0.067	N.S.	0.01	0.419	N.S.	0.000	0.890
Cynanchum chinense	Negative	0.101	**0.003**	Negative	0.126	**0.007**	Negative	0.184	**<0.001**
Phragmites australis	N.S.	0.000	0.993	Negative	0.081	**0.014**	N.S.	0.061	0.110
Artemisia capillaris	Positive	0.313	**<0.001**	Negative	0.189	**<0.001**	—	—	—
Atxiplex patens	N.S.	0.101	0.072	Negative	0.316	**<0.001**	N.S.	0.007	0.642

Abbreviation: N.S. = non-significant relationship.
Bold values indicate statistical significance at α = 0.05. '—' represents no data for testing.

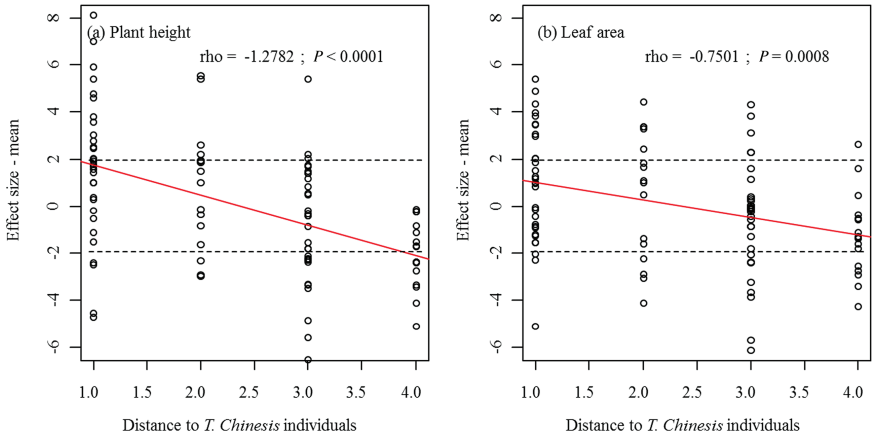

Figure 3 : rank correlation between effect sizes and distance to nearest *T. chinensis* individuals for test statistic, mean and two functional traits: (**a**) plant height, (**b**) leaf area, respectively. Distance to nearest *T. chinensis* individuals were changed into ordinal variables ranging from the nearest distance category (Class 1) to the farthest category (Class 4). Y-axes represent z-scores, and each circle corresponds to one subplot. The dashed horizontal lines at −1.96 and 1.96 indicate the significance boundaries. Solid lines represent the trend lines that identify significant correlation trajectories, with rho being the slope.

Table 4 : rank correlations between effect sizes and distance to the nearest *T. chinensis* individual for two functional traits and four test statistics

Test statistic	Plant height		Leaf area	
	rho	*P*-value	rho	*P*-value
Mean	−1.2782	**< 0.0001**	−0.7501	**0.0008**
Range	−0.3069	0.4812	−0.4851	0.1744
meanNTD	−0.0662	0.5361	−0.1588	0.1163
varNTD	−0.1901	0.2575	0.1311	0.3841

Rho is the slope of trend lines shown in Fig. 3.

In this study, we did not measure other functional traits that are related to nutrient and water acquisition; therefore, this study provides no certainty regarding how the herbaceous plant community is organized with respect to these functional traits at local scale in this supratidal wetland. Moreover, the ecological assembly rules were only studied at a small spatial scale. At larger spatial scales, such as supratidal wetland and intertidal wetland, there exists apparent environmental heterogeneity and fragmentation (Bi *et al.* 2014). Community assembly would be complicated due to spatial variability. Not only are we interested in plant community assembly in the early succession stage but also the direction of succession under the impact of anthropogenic activities, i.e. saline groundwater exploitation and seawall construction. Extensive projects in plant community ecology have been developed to 'fill the gaps' of this study and strengthen both the ecological theory and conservation management (Roura-Pascual *et al.* 2010).

The role of *T. chinensis* in shaping herbaceous plant community

Firstly, spatial structure analysis indicated that the herbaceous plant species were not randomly distributed but significantly structured. The first three canonical axes were indeed highly aligned with the spatial positions of the three

T. chinensis individuals showing the evidence of *T. chinensis* in shaping the spatial structure of herbaceous plant communities. Linear regression analysis showed that large individuals of herbaceous plant species were found closely surrounding the *T. chinensis* individuals highlighting the evidence of the facilitative effect of *T. chinensis* on the establishment of herbaceous plant species (Table 3).

There have been long-standing debates on the influence of competition on community composition across ecological gradients (Grime 1979; Taylor *et al.* 1990). Schamp and Aarssen (2009) found evidence that species organization according to maximum height changed significantly along a forest productivity gradient; specifically, the mean of species maximum height became increasingly higher than that expected by chance with the increase of forest productivity. In our study, ecological gradients induced by the presence of *T. chinensis* also exist. Rank correlation analysis showed that the mean of species height and leaf area decreased with the increase of distance to nearest *T. chinensis* individuals, suggesting that herbaceous plants were facilitated by *T. chinensis* for growing in height and leaf area. However, the effects of other test statistics, such as range, did not change significantly among distance classes, suggesting that trait convergence of some functional traits might be induced by factors other than the presence of *T. chinensis*.

In many harsh environments, e.g. subantarctic islands, desert system and high altitude mountainous areas, positive interspecific interactions are evident in plant communities, where the facilitative effect of one plant species on other plant species is provided through sheltering from strong wind (Baumeister and Callaway 2006; Carlsson and Callaghan 1991; le Roux and McGeoch 2008; Venn *et al.* 2009). In this coastal wetland, strong winds usually occur in April and May, coinciding with the early growing season of the herbaceous plant species. The woody structure of adult *T. chinensis* individuals can effectively protect grass seedlings from strong desiccating winds. Based on the above analyses, we speculated that wind sheltering effect could be a possible explanation of the positive interspecific interaction in the herbaceous plant community. Of course, there are other facilitative mechanisms that can be speculated (Bruno *et al.* 2003; Callaway 1997; Choler *et al.* 2001; Richardson *et al.* 2014; Stachowicz 2001). In conclusion, *T. chinensis* largely structured the assembly of herbaceous plant community in early succession.

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